The *n*-alkane and sterol composition of living fen plants as a potential tool for palaeoecological studies

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ABSTRACT

In groundwater-fed fen peatlands, the surface biomass decays rapidly and as a result, highly humified peat is formed. A high degree of humification constrains palaeoecological studies because reliable identification of plant remains is hampered. Organic geochemistry techniques as a means of identifying historical plant communities have been successfully applied in bog peats. The method has also been applied to fen peat, but without reference to the composition of fen plants. In this study we have applied selected organic geochemistry methods to determine the composition of neutral lipid fractions from 12 living fen plants, to investigate the potential for the distributions to characterize and separate different fen plants

and plant groups. Our results show correspondence with previous studies, e.g. C_{23} and C_{25} *n*-alkanes dominate *Sphagnum* spp. and C_{27} to C_{31} alkanes dominate vascular plants. However, we also found similarities in *n*-alkane distributions between *Sphagnum* spp. and the below ground parts of some vascular plants. We tested the efficiency of different *n*-alkane ratios to separate species and plant groups. The ratios used in bog studies (e.g. *n*-C_{23}/*n*-C_{25} and *n*-C_{23}/*n*-C_{29}) did not work as consistently on fen plants. Some differences in sterol distribution were found between vascular plants and mosses; in general vascular plants had a higher concentration of sterols. When distributions of *n*-alkanes, *n*-alkane ratios and sterols were all included as variables, redundancy analyses (RDA) separated different plant groups into their own clusters. Our results imply that the pattern in bog biomarkers cannot directly be applied to fen environments. Nevertheless, they encourage further testing to determine whether or not the identification of plant groups, plants or plant parts from highly humified peat is possible by applying fen species-specific biomarker proxies.

Keywords: biomarker, geochemistry, palaeoecology, peatland, fen, *Sphagnum*, vascular plant.

1. Introduction

Northern peatlands comprise a large store of carbon, 547 (473—621) Pg (Yu et al., 2010); acute and contemporary questions related to human-induced changes in climate have therefore emphasized the importance of thoroughly understanding peatland dynamics, past and present. Peatland carbon balance is highly sensitive to moisture conditions (e.g. Alm et al., 1999; Waddington and Roulet, 2000): the water table depth defines both the prevailing plant assemblages and the thickness of the oxic layer, where most biological production and decomposition take place. Hydrology and the source of nutrients are the main factors controlling the type of peatland and the occurrence of species (Wheeler and Proctor, 2000, Økland et al., 2001). The nutrient (trophic) level of a peatland is described as a gradient from

nutrient rich to nutrient poor: eutrophic, minerotrophic, mesotrophic, oligotrophic and ombrotrophic. Nutrient poor bogs receive water and nutrients only through precipitation while nutrient rich fens receive water and nutrients from atmospheric input, groundwater and underlying and surrounding mineral soils (Rydin et al., 2006). Bogs are characterized by dry and wet microhabitats: hummocks (surface 20-50 cm above the water table), intermediate lawns (5-20 cm above the water table) and wet flarks where the water table is at the surface, each maintaining specific plant assemblages. Fens on the other hand do not have such distinguishable microhabitat formation (Rydin et al., 2006, Laine et al., 2009). Given the vital role of vegetation in the peatland carbon budget (e.g. Riutta et al., 2007) and the fact that bryophyte and vascular plant dominated communities differ in their CO_2 and CH_4 dynamics (Laine et al., 2007, Levy et al., 2012) it is important to understand past mechanisms that have controlled the vegetation dynamics. Historical variations in climate and hydrology are preserved in peat layers as alterations in the assemblages of different biological organisms. In particular, past vegetation assemblages have been a key proxy for reconstructing past moisture conditions in a range of sites (e.g. Barber et al., 1998; Mauquoy et al., 2002; Tuittila et al., 2007; Väliranta et al., 2007). This reflects the slow and incomplete decomposition of peat in bog environments, meaning that bogs usually contain relatively well preserved plant material for palaeoecological examination. In contrast, in fen environments surface decay is rapid and a major part of the peat below the surface layer is highly humified (Moore et al., 2007). Fen peats thus tend to lack identifiable plant remains. Given that all bogs are underlain by a fen peat phase and a major proportion of the northern peatlands are still in a fen phase, there is considerable spatio-temporal restriction for palaeoecological applications based on identifiable plant remains alone.

Studies of bog peats have shown that plant biomarkers, i.e. species-specific compounds, can be successfully applied to less-humified peat to identify fossil plant groups (e.g. Xie et al., 2000; Avsejs et al., 2002; Pancost et al., 2002, 2003; Nichols et al., 2006; Jia et al., 2008; McClymont et al., 2008; Bingham et al., 2010). Different plant groups can be separated, for instance by comparing *n*-alkane distributions and ratios, e.g. the difference in concentration of low molecular weight (LMW) *n*-C_{23} and *n*-C_{25}, and high molecular weight (HMW) *n*-C_{29} and *n*-C_{33} can be used to separate contributions from *Sphagnum* and non-*Sphagnum* species (Pancost et al., 2002, Nichols et al., 2006, Vonk and Gustafsson, 2009, Lopez-Diaz et al., 2010, Ortiz et al., 2011, Andersson et al., 2011). Studies have also shown that some moss species can be distinguished down to species level (Jia et al., 2008; Bingham et al., 2010), e.g. *n*-C_{23}/*n*-C_{25} alkane ratio in bog peat may track changes in *Sphagnum fuscum* abundance (Bingham et al., 2010).

A thorough investigation of the lipid distributions in fen plants has not, to our knowledge, been performed. As a result, it is not clear whether or not the application of biomarker ratios from ombrotrophic peat plants would be a robust approach for the characterization of peatlands including fens (Andersson et al., 2011). In this study we have applied selected organic geochemical analyses to living fen plant species, excluding the litter. Specifically, we aimed to define whether or not (i) the analyses could separate bryophytes from vascular plants and (ii) there are specific fen plant proxies.

2. Material and methods

2.1. Sampling

Samples of living plants were collected from three individual but closely located fens from the Siikajoki commune (64°45´N, 24°42´E) in the mid-boreal bio-climate zone in Finland

(Fig. 1). The water level of fens is on average 10 cm below the soil surface and the pH of the water squeezed from the mosses is between 4 and 4.3. A detailed description of the sites (SJ2-4) is given by Leppälä et al. (2011) and Laine et al. (2011).

Twelve plant species typical of fens were chosen: five bryophyte species and seven vascular plant species (Table 1). Bryophytes were treated as whole plants. Vascular plants, sedges and forbes were divided into above and below ground parts because previous studies had shown that the *n*-alkane concentration might vary between different plant parts (Dawson et al., 2000, Jansen et al., 2006). In fen environments sedge and forb roots may also form a substantial contribution to the organic matter (OM) input to the upper peat (cf. Saarinen, 1996, Moore et al. 2002, Andersson et al., 2011, Huang et al., 2011). To assess methodological reproducibility we repeated the analyses with six randomly selected samples [*Sphagnum papillosum, Warnstorfia exannulata, Carex rostrata* (above and below ground parts), *Potentilla palustris* and *Menyanthes trifoliata* (above ground parts). Compound concentrations are as mean values, and the standard error of the mean (SE) is reported when the compound was found in both the original and repeated analyses. Moreover, we collected and analyzed a selection of species (*W. exannulata,* and the below ground parts of *C. rostrata, C. livida, C. nigra, C. lasiocarpa, E. angustifolium* and *M. trifoliata*) from a nearby peatland. This procedure was executed in order to test for location-related variation in compositions. Total organic carbon (TOC) was measured to test whether or not the lipid concentration between sampled plants/plant parts differed because of TOC content or concentration calculated from dry weight.

2.2. Solvent extraction

The plant parts were separated and washed with distilled water. Lipids were extracted from ca. 0.2 g of the freeze dried and ground samples using repeated ultrasonication (20 min) with 6 ml CH_2Cl_2/MeOH (3:1, v/v). Samples were saponified with 0.5 M methanolic (95%) NaOH for 2 h at 70 °C and the neutral lipids extracted using hexane. The neutral lipids were further separated into apolar and polar compounds using activated Al_2O_3 columns, eluting with hexane/CH_2Cl_2 (9:1, v/v) and CH_2Cl_2/MeOH (1:2, v/v), respectively. Prior to analysis using gas chromatography (GC) and GC-mass spectrometry (GC-MS) the polar fractions were derivatised using bis(trimethylsilyl)trifluoroacetamide (Sigma Aldrich).

2.3. GC-MS

Apolar and polar fractions were analyzed using GC-MS with the gas chromatograph equipped with flame ionisation detection (GC-FID) and split/splitless injection (280 C). Separation was achieved with a fused silica column (30 m x 0.25 mm i.d) coated with 0.25μm 5% phenyl methyl siloxane (HP-5MS), with He as carrier gas, and the following oven temperature programme: 60 – 200 °C at 20 °C/min, then to 320 °C (held 35 min) at 6°C/min. The mass spectrometer was operated in full scan mode (50-650 amu/s, electron voltage 70eV, source temperature 230 °C). Compounds were assigned using the NIST mass spectral database and comparison with published spectra (e.g. Goad and Akihisa, 1997; Killops and Frewin, 1994). Quantification was achieved through comparison of integrated peak areas in the FID chromatograms and those of internal standards of known concentration (5-α-cholestane for apolars and 2-nonadecanone for polars). Concentration values are given as concentration per dry weight of extracted material. The concentration from replicate samples was averaged in the statistical analysis.

2.4. Statistical analysis

We applied multivariate analysis to study the variation within the biomarker data. To test whether or not the variation was related to the specific plant groups or their component parts, we applied redundancy analysis (RDA) with three plant groups: mosses, above ground and below ground vascular plant parts. We conducted a series of RDA determinations. First, we analyzed the data and tested the significance separately for different variables: *n*-alkanes, *n*-alkane ratios, *n*-alcohols and sterols; we then applied RDA for different compound combinations to find the solution best explained by the three plant group variables. To link biomarker composition to plant species we included the latter as a passive variable into the analysis. A Monte Carlo permutation test was used to test the significance of the RDA solutions in all of the analyses. To make the analyses robust, compounds detected in fewer than four samples were excluded, because they might skew the result in favor of those samples in which they existed. This means that some species-specific markers were not included in the statistical analysis, but they are mentioned when individual plant analyses are discussed. The statistical analyses were conducted using Canoco for Windows 4.52 (ter Braak and Smilauer, 2002).

3. Results

We found *n*-alkanes within range of *n*-C_{17} to *n*-C_{35} in the apolar fraction. A few samples contained taraxer-14-ene, taraxast-20-ene, and an unidentified triterpanoid and taraxeroid. In the polar fraction we found sterols and *n*-alcohols. The absolute concentrations of compounds did differ between sample sets (original, repeated and replicate), but the dominance order of compounds was maintained (the full data set can be downloaded from www.pangaea.de, reference PANGAEA PDI-4071). The samples contained no evidence of bacterial activity as no traces of hopanoids or archaeol were found. A few replicate samples contained stanols and

ketones. This suggests a low level of degradation and that the samples contained compounds solely from the plants under study (e.g. Nishimura 1977, Lehtonen and Ketola 1993, Jiao et al. 2008). There was a linear correlation between concentration calculated as mass per dry weight (μg g^{-1}) and as mass per total organic carbon (μg TOC), indicating no bias due to selective preservation of OM between plant species or plant groups (Fig. 2).

3.1. Apolar fraction

The total concentration of *n*-alkanes (C_{17}-C_{35}) in moss species varied between 86.4 μg g^{-1} (*Sphagnum fimbriatum*) and 9.2 μg g^{-1} (SE 3.8) (*W. exannulata*). The distribution of *n*-alkanes of *Sphagnum* species showed an odd/even preference (Fig. 3). The C_{23} *n*-alkane dominated in *S. subsecundum* (23.6 μg g^{-1}), *S. riparium* (12.4 μg g^{-1}), and S. *papillosum* (32.6μg g^{-1}), whereas *n*-C_{25} dominated in *S. fimbriatum* (21.3 μg g^{-1}). In *W. exannulata*, C_{27} and C_{25} *n*-alkanes dominated (2.3 and 1.5 μg g^{-1}, respectively; Fig. 3). *W. exannulata* was the only moss species where taraxast-20-ene was detected (4.7 μg g^{-1}).

In above ground sedge parts an odd predominance was also present. Total *n*-alkane concentration was highest in *Carex rostrata* (332.7 μg g^{-1}, SE 44.5) and lowest in *C. nigra* (21.7 μg g^{-1}). The C_{27} *n*-alkane dominated in above ground parts of *C. livida* (7.1 μg g^{-1}), *C. nigra* (12.3 μg g^{-1}) and *Eriophorum angustifolium* (10.2 μg g^{-1}) and C_{29} in *C. rostrata* (188.8 μg g^{-1}, SE 30.8) and *C. lasiocarpa* (52.8 μg g^{-1}) (Fig. 3).

The *n*-alkane distributions in the below ground sedge parts were more complex. The short chain *n*-alkanes (C_{19}, C_{21} and C_{23}) were more abundant (Fig. 3) than the long chain *n*-alkanes (C_{27}, C_{29} and C_{31}). However, for instance, *C. nigra* had the highest concentration of *n*-C_{27} (5.2 μg g^{-1}) but the short chain *n*-alkanes were also present. In *C. lasiocarpa*, C_{23} had the highest concentration (15.7 μg g^{-1}); in *C. rostrata* the most abundant alkane was also *n*-C_{23}

(24.7 μg g^{-1}; SE 10.2). *C. livida* was dominated by *n*-C_{21} (5.7 μg g^{-1}). The below ground parts *C. lasiocarpa* was the only sample where small amounts of taraxer-14-ene (4.4 μg g^{-1}), an unidentified triterpenoid (1.5 μg g^{-1}) and taraxast-20-ene (0.6 μg g^{-1}) were found. *E. angustifolium* was dominated by *n*-C_{27} (14.7 μg g^{-1}; Fig. 3).

Menyanthes trifoliata above ground parts had the lowest total *n*-alkane concentration (5.6 μg g^{-1}; SE 0.3). In contrast, below ground plant parts had a much higher total concentration of *n*-alkanes (89.7 μg g^{-1}) than the above ground parts. Short chain *n*-C_{21} and *n*-C_{23} alkanes dominated below ground plant parts (38.0 and 25.5 μg g^{-1}, respectively), while long chain *n*-alkanes were present in small amount (Fig. 3).

In *Potentilla palustris*, the above ground and below ground parts were dominated by the long- chain *n*-alkanes and *n*-C_{31} had the highest concentration in both (497.6 μg g^{-1}, SE 182.6 and 14.7 μg g^{-1}, respectively). *Potentilla palustris* above ground parts had the highest total concentration of *n*-alkanes (985.6 μg g^{-1}; SE 350.4; Fig. 3).

3.2. n-Alkane ratios

Ratios between different *n*-alkanes have been found to be useful markers for distinguishing species in bog environments (Nott et al., 2000, Ishiwatari et al., 2005, Jansen et al., 2006, Nichols et al. 2006, Zheng et al., 2007, Vonk and Gustafsson, 2009, Bingham et al., 2010, Andersson et al., 2011). The ratios calculated here were used in these studies.

Below ground parts of *Carex nigra*, *C. livida* and *C. lasiocarpa* showed the highest *n*-C_{23} / *n*-C_{25} (ca. 5 to 7) ratio, whereas *Sphagnum* spp. had lower values (ca. 0.6 to 3). The ratios *n*-C_{23}/*n*-C_{27}, *n*-C_{23}/*n*-C_{29} and *n*-C_{23}/*n*-C_{31} were all low for the above ground plant parts (around 0) and high in *Sphagnum* species (> 10), especially *S. papillosum*. However, *n*-C_{23}/*n*-C_{27} for

C. lasiocarpa below ground parts (ca. 20) and n-C_{23}/n-C_{29} and n-C_{23}/n-C_{31} for *M. trifoliata* (ca. 40 and 70 respectively) were higher than the values in *Sphagnum* spp. The n-C_{25}/n-C_{29} ratio had a similar distribution pattern to the three above ratios, but with smaller values and more complex distribution in *Sphagnum* spp. (ca. 6 to 15). *Potentilla palustris* above ground and below ground parts were clearly separated from other samples via n-C_{31}/n-C_{27} (> 5) and n-C_{31}/n-C_{29} (PANGAEA PDI-4071).

The n-C_{23}/(n-C_{23} + n-C_{29}) and n-C_{25}/(n-C_{25} + n-C_{29}) ratios distinguished *Sphagnum* spp. as their own group (ca. 0.9). The pattern was clearest for n-C_{25}/(n-C_{25} + n-C_{29}) where *Sphagnum* spp. ratio values (> 0.8) consistently exceed higher plant values, excluding *M. trifoliata* below ground parts, which was equals to moss values (Fig.4). For n-C_{23}/(n-C_{27}+ n-C_{31}), *M. trifoliata* had the highest value (ca. 11), and *S. papillosum* stood out owing to a higher value(ca. 9) than the rest of the mosses and vascular plants. P_{aq} [(n-C_{23}+ n-C_{25})/(n-C_{23}+ n-C_{25}+ n-C_{29}+ n-C_{31})] did not seem to separate plant species. However, *S. fimbriatum* and *S. papillosum* had higher P_{aq} values (ca. 1) than the rest of the samples. P_{wax} [(n-C_{27} n-+ n-C_{29} + C_{31})/(n-C_{23}+ n-C_{25} + n-C_{27} + n-C_{29} + n-C_{31})] showed low values for *Sphagnum* spp. and *M. trifoliata* and *C. lasiocarpa* below ground parts (max. 0.2) and high values for most of the vascular plant above ground parts, and *W. exannulata* (> 0.8; PANGAEA PDI-4071).

According to previous studies the average n-alkane chain length (ACL) should separate mosses and vascular plant leaves from each other (Zhou et al., 2005). In our samples the ACL of the mosses and below ground plant parts, except *E. angustifolium* and *C. nigra*, was < 26. Vascular plant above ground parts recorded ACL values > 26 (Fig. 4).

3.3.Polar fraction

The *n*-alcohol concentration had only minor differences between different plant types and the dominant compounds often overlapped. Among the *Sphagnum* mosses the total concentration of sterols was 2100 to 2600 μg g^{-1}. It seems that *Sphagna* had no dominant sterol, but generally similar contributions from campesterol [campest-5-en-3β-ol], stigmasterol [(24*E*)-stigmasta-5,22-dien-3β-ol] and β-sitosterol [(3β)-stigmast-5-en-3-ol] were observed. Brassicasterol [(22*E*)-ergosta-5,22-dien-3β-ol], 24-methylcholest-7-en-3β-ol, obtusifoliol [4α,14α-dimethyl-5α-ergosta-8,24(24^1)-dien-3β-ol], ergost-8,24(28)-dien-3β-ol were typical for *Sphagnum* spp., but were occasionally also detected in small amounts in some of the vascular plants. *W. exannulata* samples were also characterized by high concentrations of campesterol, stigmasterol and β-sitosterol but, in contrast to the *Sphagnum* spp., obtusifoliol was not detected and the concentration of phytol was clearly highest (2035.9 μg g^{-1}, SE 913.3, but 437.9 μg g^{-1}_{rep}) among all the mosses. Gramisterol [4α-methyl-5α-ergosta-7,24(24^1)-dien-3β-ol], albeit in low concentration (ca. 10-60 μg g^{-1}), was detected in all the mosses but not the vascular plants (Table 2).

All vascular plant below ground parts, excluding *C. nigra*, had a higher concentration of sterols than above ground parts. Above parts were dominated by β-sitosterol, with the occasional presence of the associated stanol (3-stigmastanol) and cycloartenol (5α-cycloart-24-en-3β-ol). Sedge below ground parts were similar to the above ground parts, only with a smaller amount of phytol [(3,7,11,15-tetramethylhexadec-2-en-1-ol; ca. 10-60 μg g^{-1}] and higher amount of lupeol [5α-lup-20(29)-en-3β-ol; 20-250 μg g^{-1}]. *M. trifoliata* above and below ground parts were dominated by stigmasterol (1483.6 μg g^{-1} and 3647.4 μg g^{-1}). β-sitosterol and obtusifoliol were absent from all *M. trifoliata* samples, whereas the schottenol [5α-stigmast-7-en-3β-ol] was present only in *M. trifoliata* samples (above ground 678.0 μg g^{-1} and below ground 1029.4 μg g^{-1}; PANGAEA PDI-4071).

Tocopherols-δ and -γ [(2*R*)-2,8-dimethyl-2-((4*R*,8*R*)-4,8,12-trimethyltridecyl)-6-chromanol and (2*R*)-2,7,8-trimethyl-2-(4*R*,8*R*)-4,8,12-trimethyltridecyl)-6-chromanol, respectively] were only detected in *M. trifoliata*: in above ground parts tocopherol-δ 44.1 μg g^{-1} (SE 41.8) and tocopherol- γ 20.5 μg g^{-1}, and from both original and replicate below ground part samples tocopherol-δ 288.4 (SE 41.8) and 100.4_{rep} μg^{-1}, and tocopherol- γ 40.2 and 225.8_{rep} μg g^{-1}. Triterpenoids were present in *M. trifoliata* and the highest concentration was in *M. trifoliata* below ground parts (788.8 μg g^{-1}). *Potentilla palustris* above and below ground parts were dominated by β-sitosterol, below ground parts having more than double the concentration as the above ground parts (4767.8 μg g-1 and 1945.6, SE 196.4, respectively) (PANGAEA PDI-4071).

Phytol was recorded in every sample. Above ground parts of both sedges and *M. trifoliata* were dominated by phytol, the concentration being highest in *C. nigra* above ground parts (7510.9 μg g^{-1}), while below ground parts had a lower concentrations (sedges ca. 7 to 35 μg g^{-1}; *M. trifoliata* 297.4μg g^{-1}).

3.4. RDA results

RDA showed that the variation in each compound type (*n*-alkanes, *n*-alkane ratios, *n*-alcohols and sterols) was related to plant components (Table 2).

We found that the best result was achieved by combining *n*-alkanes, *n*-alkane ratios and sterols in one analysis. Monte Carlo permutation test of the RDA solution showed that all canonical axes were significant (T 0.245, F 2.597, *p* 0.0020) and the three variables explained 25% of the variance. Analysis separated mosses and vascular plants as their own clusters along the first axis. Vascular plant below ground parts and mosses, however, partly

overlapped over axis 1. Mosses formed a more compact cluster than vascular plants that was also distributed along axis 2. The second axis reflected the differences between the below and above ground parts; they were separated to the opposite ends of the axis (Fig. 5b.).

We present compounds which explained > 20% of variation detected in plants position in ordination, i.e. 30 compounds (Fig. 5a.). Compounds such as lupeol, 3-stigmastanol and β-sitosterol seemed to be descriptive for vascular plants in general. Vascular plant above ground parts were characterized by *n*-alkanes in the range *n*-C_{26} to *n*-C_{29}, *n*-C_{23}/*n*-C_{21} and the phytol concentration (Fig.5a.). The bryophyte cluster seemed to be formed on the basis of ergost-8,24(28)-dien-3β-ol, obtusifoliol, and *n*-C_{25}/*n*-C_{29} (Fig.4b.). Some compounds, such as the C_{23} *n*-alkane, several *n*-alkane ratios and brassicasterol, commonly detected in vascular plant below ground parts and in mosses, plotted mid-way between these two groups (Fig.5a, b). The *n*-C_{23}/*n*-C_{25} ratio, and lupeol and β-sitosterol concentrations were the main patterns describing, and consequently separating, vascular plant below ground parts from mosses (Fig. 5a, b).

4. Discussion

Our results support the observation that, by using *n*-alkane ratios, different plant group contributions to peat can be separated (Nott et al. 2000, Ishiwatari et al., 2005, Jansen et al., 2006, Nichols et al., 2006, Zheng et al., 2007, Vonk and Gustafsson, 2009, Bingham et al., 2010, Andersson et al., 2011). However, they also showed that, when a wider combination of plants and peat habitats is included, the absolute values which affect ratios and the relationships between plant types can change. For most of the ratios tested, vascular plant above ground parts and mosses were separated as different groups. When the contribution of the vascular plant below ground parts were taken into consideration, the published *n*-alkane

ratios for bog peat plants were less able to separate vascular plants from *Sphagnum* spp., due to overlap in the distribution patterns between *Sphagnum,* sedge and *M. trifoliata* below ground parts. Some ratios, such as n-C_{23}/n-C_{27} (Fig. 4) may potentially be used to separate *S. papillosum* from other *Sphagnum* spp. but the probable existence of vascular plant below ground parts in peat might lead to false conclusions about the prevailing vegetation assemblage. The n-C_{23}/n-C_{25} ratio, which has been applied in previous studies (e.g. Bingham et al., 2010) as a marker for *Sphagnum* spp., seems to be effective for the fen environment for separating below ground parts (< 3) from other plants sampled (>3) (Fig. 4). Based on the P_{wax} ratio, it might be possible to separate vascular plant above ground parts with lower values (< 0.9) from below ground parts and *Sphagnum* spp. (Fig. 4); this agrees with Zheng et al. (2007), who connected high (0.7) P_{wax} values with dry conditions in peat. Thus, where the P_{wax} ratio can be measured, we would predict a high contribution of vascular plant above ground material, which is consistent with a drier environment (Strak et al. 2006).

Our P_{aq} results agree with Ficken et al. (2000): we found similar values for most of the higher plant above ground parts (< 0.1; PANGAEA PDI-4071), while mosses and below ground parts gave values (0.4-1) close to plants in wet habitats (submerged and floating plants in lake ecosystems) as in Ficken et al. (2000). Due to the high concentration of C_{31} n-alkane, the n-C_{31}/n-C_{29} and n-C_{31}/n-C_{27} ratios show potential for distinguishing *P. palustris* from other species. This corresponds to some previous studies describing n-C_{31} as a marker for higher plants (Jansen et al., 2006).

Our results agree with previous studies of bog peats which have shown that LMW n-alkanes (n-C_{23} and n-C_{25}) are important biomarkers for *Sphagnum* spp. and HMW n-alkanes (n-C_{27} to n-C_{31}) for above ground parts of vascular plants (Ficken et al., 1998; Baas et al., 2000; Pancost et al., 2002; Nichols et al., 2006). Furthermore, they agree with findings that the n-

alkane distribution and concentration in vascular plant below ground parts differ from those of above ground parts (Huang et al., 2011, Dawson et al., 2000, Pancost et al., 2002, Jansen et al., 2006). ACL could also be a useful proxy for separating *Sphagnum* spp. from vascular plants in fen environments (Zhou et al., 2005, Andersson et al., 2011). The LMW *n*-alkane distribution in vascular plant roots has been addressed before and, like studies related to *Sphagnum.*spp., the dominance of LMW *n*-alkanes, e.g. *n*-C_{23}, seems to be related to wet environments (Huang et al., 2011, Xie et al., 2004). Huang et al. (2012) concluded that plants growing in water saturated conditions are unlikely to synthesize longer chain *n*-alkanes in order to prevent water loss. Thus, the presence of LMW *n*-alkanes is consistent with the presence of wet conditions. An additional complicating issue in terms of palaeoecological application is that C_{23} has also been found in significant concentration in *Betula* spp. leaves (Sachse et al., 2006).

Non species-specific or group-specific *n*-alcohol markers were detected, and the dominant homologue within one group varied. Although *n*-alcohols can be distinguished they have not been shown to have great potential when compared with other biomarkers (e.g. Xie et al., 2004). Our study revealed that potential plant group-specific markers may be found among sterols such as gramisterol, which was found only in mosses, and tocopherols and schottenol, which were found only in *M. trifoliata,* and lupeol which was not detected in any of the mosses. Otherwise, most of the sterols were commonly present in most of the samples, although concentrations differed considerably, e.g. in the case of β-sitosterol. In agreement with Huang et al. (2011) we detected a higher concentration of sterols in the vascular plant below ground parts than in above ground parts. For sterol distributions to be used as a proxy for past vegetation inputs to a fen environment, it is important that either the original sterol or corresponding degradation product(s) can be identified within core materials. It has been shown that microbial hydrogenation of sterols within peats can lead to the production of

359 stanols from the original Δ^5-sterols (e.g. Andersson and Meyers, 2012). It might be expected
360 that with greater degradation of organic matter in a fen environment there will be greater
361 transformation of sterols to stanols. However, if both the sterols and their corresponding
362 stanols can be identified and quantified in a fen core, it may be possible to both assess the
363 degree of organic matter degradation and identify the original vegetation contributions to the
364 peatland. This requires further testing, but our data suggest that, if sterols and stanols are
365 present in peat, they may provide additional information about the contributing vegetation
366 (Meyers 2003).

367 The differences detected between mosses and vascular plants, as well as the similarities
368 between *Sphagnum* spp. and below ground vascular plant parts could spring from the
369 differences in the surrounding hydrological conditions. Mosses and below ground plant parts
370 are under the influence of stagnant water in fens, where the water table can be close to the
371 mire surface throughout the growing season (Laine et al., 2012). These plants and plant parts
372 in fens might therefore produce wax with a higher abundance of LMW *n*-alkanes for
373 protection against micro-organisms and degradation than in moderately drier habitats, i.e.
374 bogs. In the future, one way to study the source of water and the hydrological environment of
375 different *n*-alkanes in peat is to examine the δD values of different plant *n*-alkanes (e.g. Xie et
376 al., 2004, Nichols et al., 2010, Garcin et al., 2012).

377 The data presented here shows that there are differences in biomarker distributions between
378 fen plants, but also between species which live in fens and bogs. This means that the
379 application of biomarker distributions from plants living in bog environments to cores from
380 fens could give mis-leading information about past vegetation contributions. In order to apply
381 the data presented here to a fen environment may not be straightforward, however. Although
382 some promising individual biomarkers were found, a better way to identify species and plant

groups appeared to be to combine the variables and apply constrained multivariate analysis, such as RDA, as applied here. As a result of the similarity in *n*-alkane distributions, and consequently *n*-alkane ratios, similarities between mosses and vascular plant below ground parts remained apparent, but the differences in sterol compositions separated these two groups (Fig. 5b). As a result of our investigations, we would recommend that potential target ratios or markers for down-core analyses might include: (i) lupeol and a high concentration of β-sitosterol, together with $n\text{-}C_{23}/n\text{-}C_{25} > 3$, for prevalence of vascular plant below ground parts; (ii) high $n\text{-}C_{23}/n\text{-}C_{31}$ value, combined with the presence of obtusifoliol and gramisterol to indicate the presence of *Sphagnum* mosses; and (iii) a high concentration of HMW *n*-alkanes, as in previous studies, for a dominance of vascular plant above ground parts. The degradation of the compounds, especially sterols, has to be considered as they might not be preserved in fen environments, due to a high rate of humification or possible transport in the system. A detailed study of this matter is in progress. The effect of peat humification on lipid concentration should also be taken into account by calculating concentration relative to TOC content. This procedure normalizes the results so that different layers with different extent of degradation become more comparable (Meyers 2003; Ortiz et al., 2010). Given the freshness of our samples, this did not impact on our results, but should be considered for palaeo-studies.

5. Conclusions

We found no clear difference in the sterol composition of the living fen plants but, when comparing *n*-alkanes and their ratios, vascular plant above ground parts could be separated from mosses. However, due to the similar *n*-alkane composition between most of the vascular plant below ground parts and mosses and consequently similar *n*-alkane ratios, separating

these two groups from highly humified peat can be challenging. When *n*-alkanes, their ratios and sterols of the plants were compared, together with redundancy analysis, three groups were formed: mosses, above ground and below ground. Thus RDA, or a comparable approach, has potential for also differentiating plant groups in fossil peats. Our results also show that the existing biomarker proxies for peatlands are challenged when a wider combination of plants and peat environments is taken into account.

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584

585 **Captions:**

586 **Fig. 1.** Map of study site. Samples were collected from the fens of the Siikajoki commune
587 (64°45´N, 24°42´E), Finland, Northern-Europe.

588

589 **Fig. 2.** Correlation between concentration μg g^{-1} dry wt and μg g^{-1}TOC. R^2 values of
590 compared variables: *n*-C_{23} 0.99, *n*-C_{31} 1, β-sitosterol 0.99, campesterol 0.99.

591

592 **Fig.3.** Concentration (μg g^{-1} dry wt.) for C_{17} -C_{35} *n*-alkanes of plants. Mosses (top), above
593 ground and below ground parts of sedges (middle) and forbes (bottom) are shown. Black bars

represent original samples, samples which were re-analyzed have error bars and samples which were replicated are represented with white bars.

Fig. 4. Ratios of *n*-alkanes for mosses and (A) above ground and (B) below ground parts of sedges and forbes: $n\text{-}C_{23}/n\text{-}C_{25}$ (Bingham et al., 2010), $C_{23}/n\text{-}C_{27}$, $n\text{-}C_{23}/n\text{-}C_{31}$ (Nott et al., 2000), n- $n\text{-}C_{23}/(n\text{-}C_{23} + n\text{-}C_{29})$ (Nichols et al., 2006), $n\text{-}C_{25}/n\text{-}C_{29}$ (Jansen et al., 2006), $n\text{-}C_{31}/n\text{-}C_{27}$ (Janssen et al., 2006) and P_{wax} (Zheng et al., 2007) and ACL of the plant components. Values of $n\text{-}C_{23}/n\text{-}C_{31}$ for *Warn. exannulta*, *Carex nigra* and *C. lasiocarpa* below ground parts are 0. For ACL, *Sphagnum papillosum*, *Carex rostrata* above ground and below ground parts and *P. palustris* and *M. trifoliata* below ground parts standard error of mean is < 0.5.

Fig. 5. RDA (F-ratio 2.597, *p*-value 0.002) shows the distribution of *n*-alkanes, *n*-alkane ratios, sterols and sampled plants (A, above-ground; B, below-ground). Groups: moss, above ground and below ground plant parts, were used as environmental variables. Only compounds with a fit of > 20% are shown (altogether 30 compounds).

Table 1

Studied plants and their status along the nutrient gradient from poor to rich: ombro-, oligo-, meso-, minero-, eutrophic, and their typical location in microhabitats from dry to wet: hummock, lawn, flark.

Table 2

617 Results RDA with Monte Carlo permutation test to test the significance of plant components:

618 mosses, leaves and roots for the variation in compounds [a].


70°N
0°
10°E
20°E
30°E
40°E
0
250
500
1 000 km
Siikajoki
Finland
Russia
60°N
50°N

Fig 1.

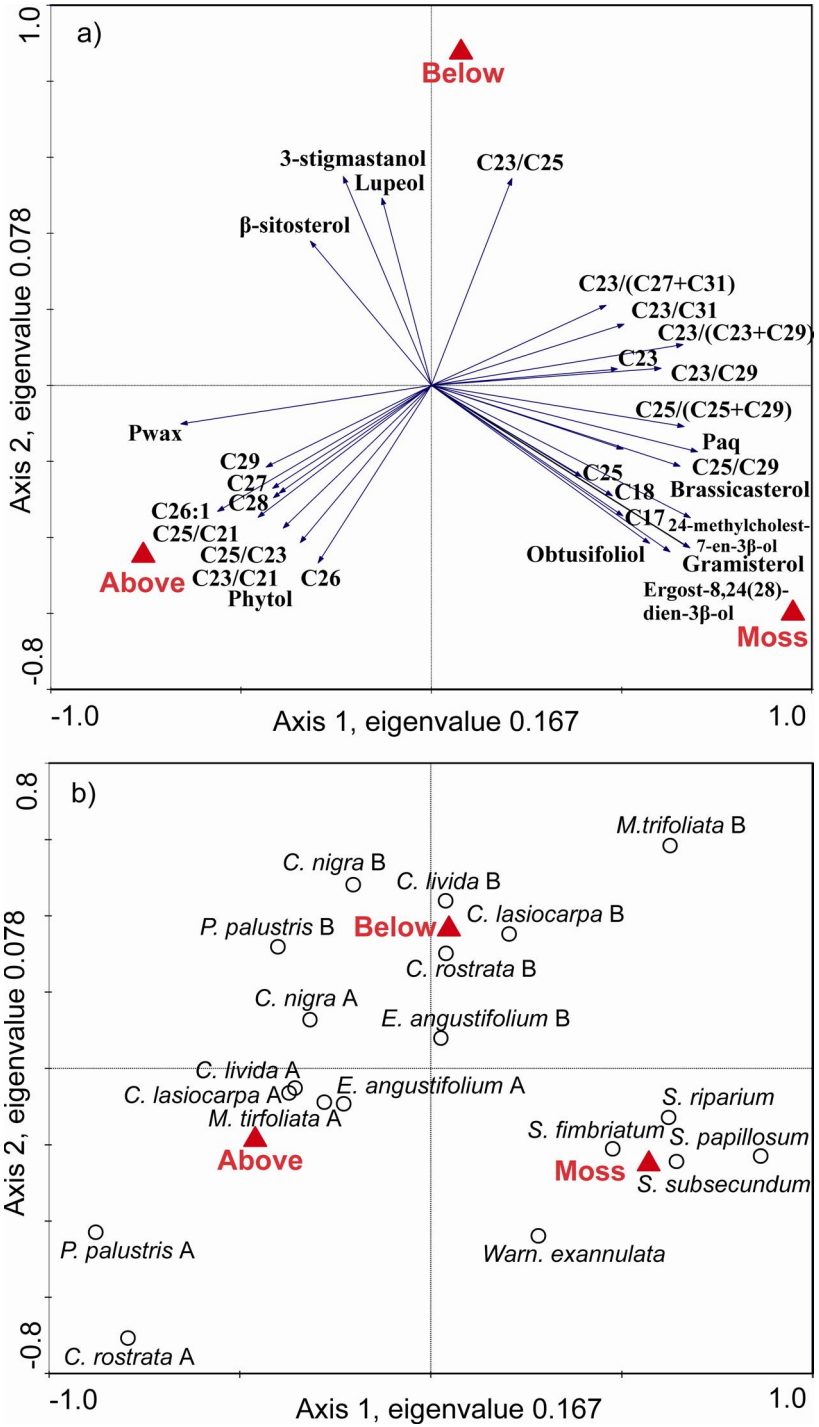
a)
Below
3-stigmastanol
Lupeol
C23/C25
β-sitosterol
C23/(C27+C31)
C23/C31
C23/(C23+C29)
C23
C23/C29
C25/(C25+C29)
Pwax
Paq
C29
C25/C29
C27
C25
C18
Brassicasterol
C28
C26:1
C17
24-methylcholest-7-en-3β-ol
C25/C21
Obtusifoliol
C25/C23
Gramisterol
Above
C23/C21
C26
Ergost-8,24(28)-dien-3β-ol
Phytol
Moss
Axis 2, eigenvalue 0.078
1.0
-0.8
-1.0
Axis 1, eigenvalue 0.167
1.0

Fig 4.

b)
M.trifoliata B
C. nigra B
C. livida B
C. lasiocarpa B
P. palustris B
Below
C. rostrata B
C. nigra A
E. angustifolium B
C. livida A
E. angustifolium A
C. lasiocarpa A
S. riparium
M. tirfoliata A
S. fimbriatum
S. papillosum
Above
Moss
S. subsecundum
P. palustris A
Warn. exannulata
C. rostrata A
Axis 2, eigenvalue 0.078
0.8
-0.8
-1.0
Axis 1, eigenvalue 0.167
1.0

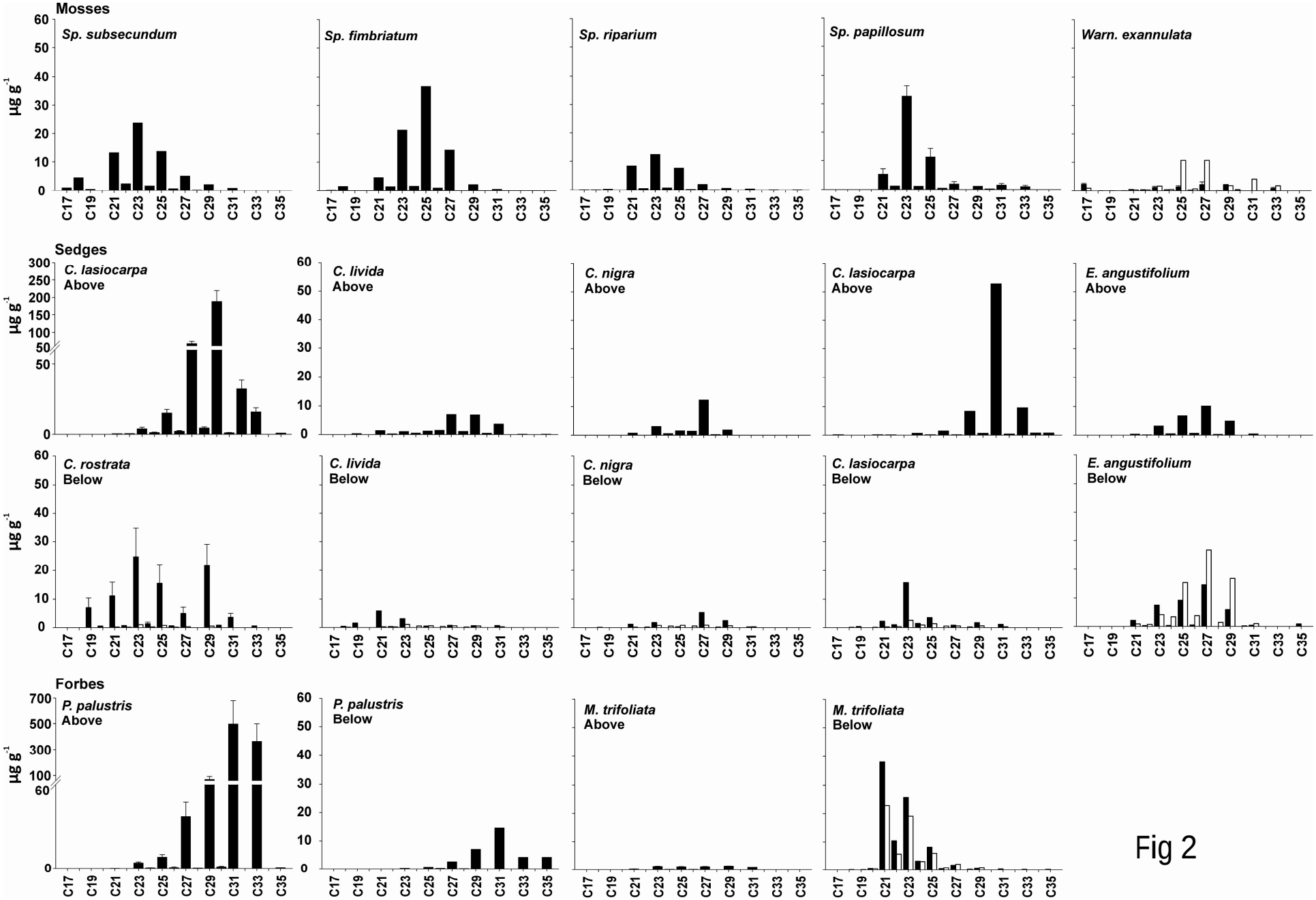
Mosses
Sp. subsecundum
Sp. fimbriatum
Sp. riparium
Sp. papillosum
Warn. exannulata
Sedges
C. lasiocarpa
Above
C. livida
Above
C. nigra
Above
C. lasiocarpa
Above
E. angustifolium
Above
C. rostrata
Below
C. livida
Below
C. nigra
Below
C. lasiocarpa
Below
E. angustifolium
Below
Forbes
P. palustris
Above
P. palustris
Below
M. trifoliata
Above
M. trifoliata
Below
µg g-1
C17 C19 C21 C23 C25 C27 C29 C31 C33 C35

Fig 2

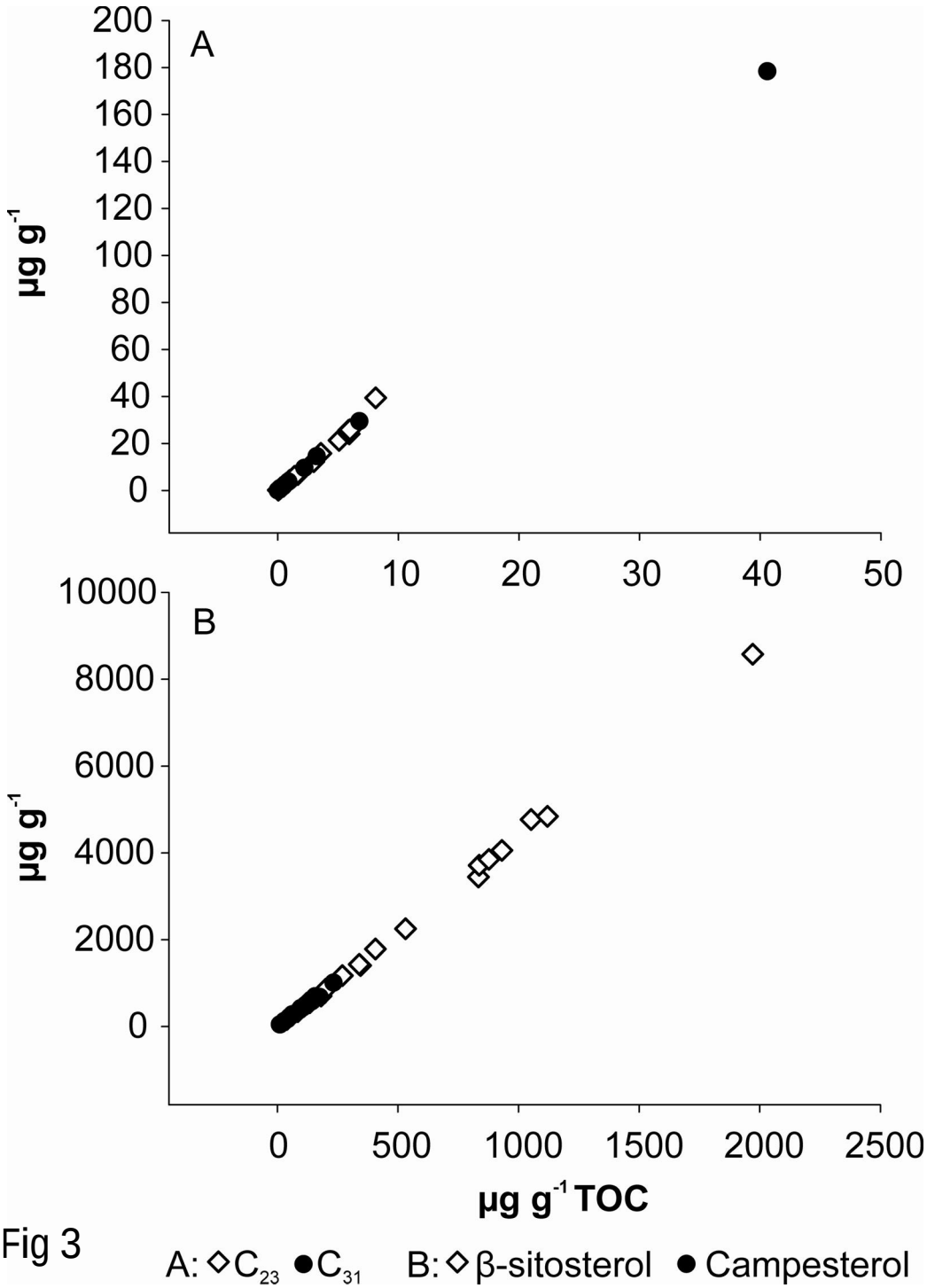

Fig 3

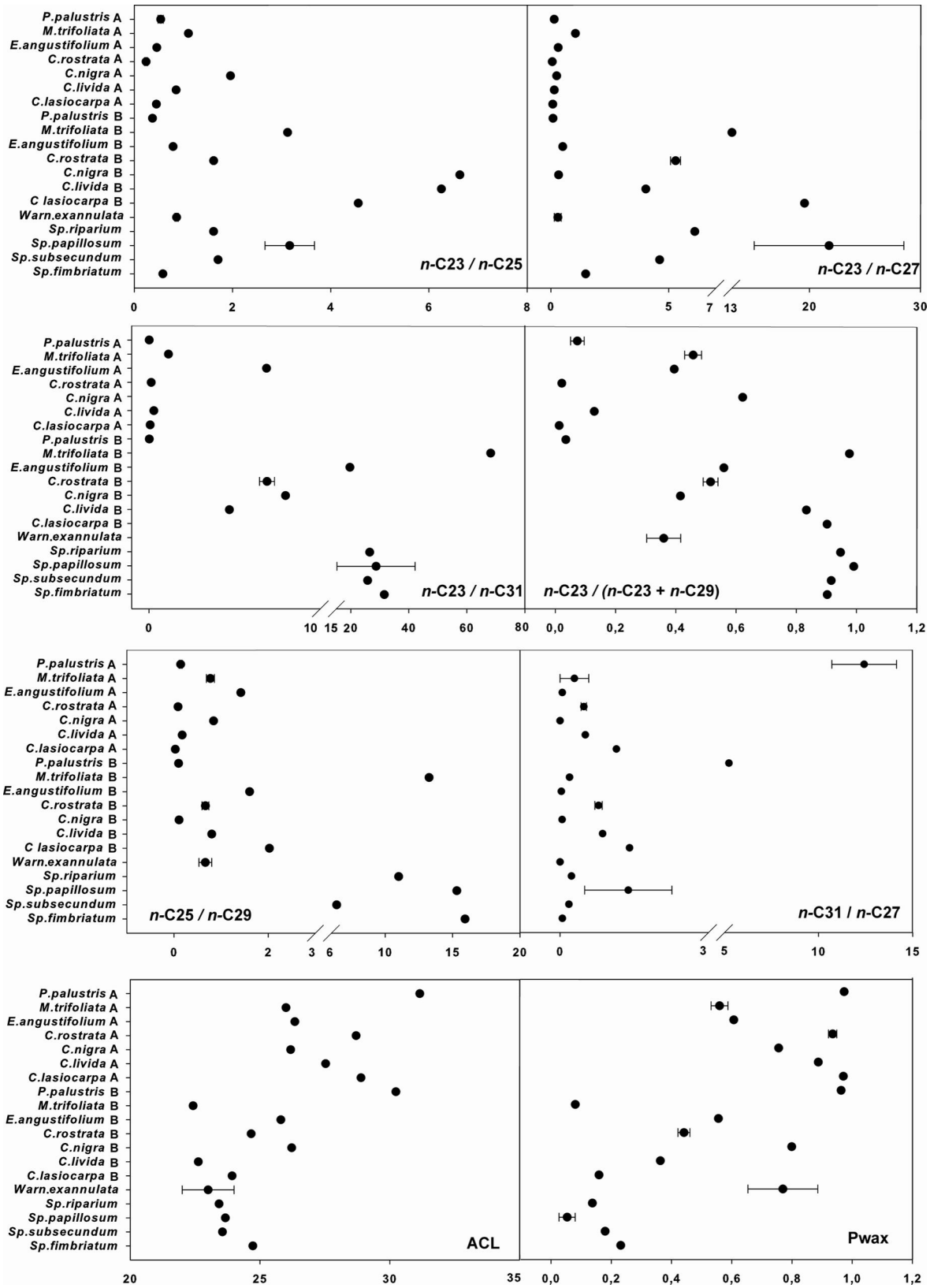
P.palustris A
M.trifoliata A
E.angustifolium A
C.rostrata A
C.nigra A
C.livida A
C.lasiocarpa A
P.palustris B
M.trifoliata B
E.angustifolium B
C.rostrata B
C.nigra B
C.livida B
C lasiocarpa B
Warn.exannulata
Sp.riparium
Sp.papillosum
Sp.subsecundum
Sp.fimbriatum
n-C23 / n-C25
0 2 4 6 8
n-C23 / n-C27
0 5 7 13 20 30
n-C23 / n-C31
0 10 15 20 40 60 80
n-C23 / (n-C23 + n-C29)
0,0 0,2 0,4 0,6 0,8 1,0 1,2
n-C25 / n-C29
0 2 3 6 10 15 20
n-C31 / n-C27
0 3 5 10 15
ACL
20 25 30 35
Pwax
0,0 0,2 0,4 0,6 0,8 1,0 1,2

Fig 3.